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Climate teleconnections synchronize *Picea glauca* masting and fire disturbance: evidence for a fire-related form of environmental prediction

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Abstract

1. Synchronous pulses of seed masting and natural disturbance have positive feedbacks on the reproduction of masting species in disturbance-prone ecosystems. We test the hypotheses that disturbances and proximate causes of masting are correlated, and that their large-scale synchrony is driven by similar climate teleconnection patterns at both inter-annual and decadal time scales.

2. Hypotheses were tested on white spruce (*Picea glauca*), a masting species which surprisingly persists in fire-prone boreal forests while lacking clear fire adaptations. We built masting, drought and fire indices at regional (Alaska, Yukon, Alberta, Quebec) and subcontinental scales (western North America) spanning the second half of the 20th century. Superposed Epoch Analysis tested the temporal associations between masting events, drought and burnt area at the regional scale. At the sub-continental scale, Superposed Epoch Analysis tested whether El Niño-Southern Oscillation (ENSO) and its coupled effects with the Atlantic Multidecadal Oscillation (AMO) in the positive phase (AMO+/ENSO+) synchronize drought, burnt area and masting. We additionally tested the consistency of our synchronization hypotheses on a decadal temporal scale to verify whether long-term oscillations in AMO+/ENSO+ are coherent to decadal variation in drought, burnt area and masting.

3. Analyses demonstrated synchronicity between drought, fire and masting. In all regions the year before a mast event was drier and more fire-prone than usual. During AMO+/ENSO+ events sub-continental indices of drought and burnt area experienced significant departures from mean values. The same was observed for large-scale masting in the subsequent year, confirming 1 year lag between fire and masting. Sub-continental indices of burnt area and

masting showed in-phase decadal fluctuations led by the AMO+/ENSO+. Results support the "Environmental prediction hypothesis" for mast seeding.

4. *Synthesis*. We provide evidence of large-scale synchronicity between seed masting in *Picea glauca* and fire regimes in boreal forests of western North America at both inter-annual and decadal time scales. We conclude that seed production in white spruce predicts changes in disturbance regimes by sharing the same large-scale climate drivers with drought and fire. This gives new insides in a mechanism providing a fire-sensitive species with higher than expected adaptability to changes in climate.

Key-words: reproduction ecology, fire regime, mast seeding, ENSO, AMO, environmental prediction hypothesis, economy of scale, fire ecology, climate change

Abstract in French

1. La synchronisation du masting des semis et des perturbations naturelles ont un effet positif sur la reproduction d'espèces à fructification irrégulière dans des écosystèmes sensibles aux perturbations. Dans cette étude, on a testé les hypothèses qu'il existait une corrélation entre les perturbations et les causes ultimes du masting et que leurs synchronisations à grande échelle était dû à des patrons de téléconnections climatiques similaires, aux échelles décennales et interannuelles.

2. L'espèce cible choisie pour tester cette hypothèse est l'épinette blanche (Picea glauca) une espèce à fructification irrégulière qui inopinément réussit à survivre dans les forêts boréales de l'Amérique du nord. On a créé des indices de masting, de sécheresse et de feux de forêt à des échelles régionales (Alaska, Yukon, Alberta, Québec) et subcontinental (Nord-ouest de l'Amérique du nord) pour la deuxième moitié du XX siècle. L'association temporelle à l'échelle régionale entre masting, sécheresse et feux a été testée par le biais d'une analyse par époques superposées (Superposed Epoch Analysis). Au niveau subcontinental, la Superposed Epoch Analysis a été utilisée pour tester si la ENSO (El Niño-Southern Oscillation) et ses effets cumulatifs avec l'AMO (Oscillation Atlantique Multi décennale) pendant des phases positives (AMO+/ENSO+) synchronisent le masting, la sécheresse et les feux. La constance de ses

synchronisations a été testée sur une échelle temporelle décennale pour vérifier si les oscillations AMO+/ENSO+ sur le long terme étaient cohérente avec les variations des sécheresses, des surfaces brulées et du masting.

3. Les analyses ont révélé la synchronisation entre sécheresse, feux et masting. Dans toutes les régions, l'année qui précède un phénomène de masting a été sèche et plus propice aux incendies que d'habitude. Pendent les épisodes AMO+/ENSO+, les indices de sécheresse et de surface brulée à l'échelle subcontinentale ont montré des valeurs hors de la moyenne. De même, les phénomènes de masting à large échelle qui ont eu lieu dans l'année suivante, confirment le décalage d'un an entre les feux et la production de semis. Les résultats supportent l'hypothèse d'une prédiction environnementale (*Environmental prediction hypothesis*) pour le masting comme démontré avec la fluctuation parallèle sur une échelle décennale de la surface brûlée et du masting au niveau subcontinentale.

4. En synthèse, on a prouvé la synchronisation à grande échelle entre les événements de masting de Picea glauca et le régime des feux de couronne dans les forêts boréales du nord-ouest de l'Amérique du nord, que ce soit à des rythmes interannuelles ou décennales. La production abondante de semis chez l'épinette blanche, étant stimulée par les mêmes facteurs qui règlent la sécheresse et les incendies, suit donc les changements du régime des perturbations. Cela nous donnent de nouvelles connaissances sur un mécanisme qui permet à une espèce sensible au feu d'avoir un potentiel d'adaptation au changement climatique plus haut que prévu.

Introduction

Climate teleconnections are recurring large-scale patterns of air pressure and circulation anomalies that span large geographical areas (Nigam & Baxter, 2015). In ecology, teleconnections are a relevant phenomenon since they synchronize environmental features such as precipitation, temperature, wind patterns and related geophysical and ecological phenomena through space and time (Mysterud, Stenseth, Yoccoz, Ottersen, & Langvatn, 2003). Showing both yearly variability and long-term oscillatory trends that arise from the non-linear dynamics of the coupled system, teleconnections have cascading effects on ecosystems and organisms at both inter-annual and decadal time scales (Beck, Fletcher, Gadd, Heijnis, & Jacobsen, 2017; Stenseth et al., 2002).

As these climate patterns affect all phenomena simultaneously and force them to fluctuate in synchrony (Liebhold, Koenig, & Bjørnstad, 2004), direct and indirect interactions between organisms and their physical environment emerge (Forchhammer & Post, 2004). So for instance, teleconnections affect both natural disturbance regimes (Mariani, Veblen, & Williamson, 2018; Shabbar & Skinner, 2004) and yearly to decadal fluctuations in large-scale reproduction pulses in seed-masting species (Ascoli, Vacchiano, et al., 2017; Chechina & Hamann, 2019; Strong, Zuckerberg, Betancourt, & Koenig, 2015; Williamson & Ickes, 2002). In-phase fluctuations of seed pulses and disturbance have important consequences for the regeneration dynamics of masting species. Disturbances often promote environmental conditions that favor seed germination, seedling emergence and establishment, including exposed soil, increased light at the forest floor, and low competition by concurring vegetation (Pickett & White, 1985). However, within a few years post-disturbance, these favorable conditions might get lost. Therefore, the timing of reproduction relative to disturbance is key for successful regeneration (Greene et al., 2007; Peters, Macdonald, & Dale, 2005; Maringer et al., 2020; Purdy, Macdonald, & Dale, 2002; van Mantgem, Stephenson, & Keeley, 2006).

Several disturbance-adapted species have evolved strategies to reproduce soon after severe disturbance in order to obtain a competitive advantage – for example, resprouting or serotiny in fire-prone ecosystems subject to crown-fire regimes (He, Belcher, Lamont, & Lim, 2016; Veraverbeke et al., 2014). Consequently, when disturbance-adapted species co-occur with masting-obligate seeders, the latter will be competitive only when masting occurs shortly after

the disturbance (Ascoli, Vacchiano, Maringer, Bovio, & Conedera, 2015; Frey, Ashton, McKenna, Ellum, & Finkral, 2007; Marod, Kutintara, Tanaka, & Nakashizuka, 2002; O'Dowd & Gill, 1984; Wright, Zuur, & Chan, 2014).

Given that both masting and natural disturbances are influenced by large-scale climate patterns (Koenig & Knops, 1998; Seidl et al., 2017), this suggests that the two processes may be related, so as climate patterns conducive to severe large-scale natural disturbances also act as proximate causes of masting synchronizing seed crops over wide areas (Pearse, Koenig, & Kelly, 2016; Bogdziewicz et al. 2019). In such synchronous fluctuation of the two phenomena through space and time, masting species would gain a competitive advantage in disturbance-prone ecosystems (Ascoli , Vacchiano, et al., 2017; Williamson & Ickes, 2002).

Here we test the hypotheses that natural disturbances and proximate causes of masting are correlated, and that the large-scale synchrony of these phenomena are driven by similar large-scale climate drivers (teleconnections) at both inter-annual and decadal time scales. We selected the boreal forest of North America, a biome where disturbances are well-recorded and mainly driven by natural agents. In these area, the fire regime follows relatively natural cycles of drought and lightening-induced ignitions (Fauria & Johnson, 2006; Hess, Scott, Hufford, & Fleming, 2001; Veraverbeke et al., 2014), driven by large-scale climate patterns at both inter-annual and decadal time scales (Kitzberger, Brown, Heyerdahl, Swetnam, & Veblen, 2007; Shabbar & Skinner, 2004). As study species we chose the obligate-seeder white spruce (*Picea glauca* (Moench) Voss) that persists in a fire-prone environment subjected to a crown-fire regime despite its masting strategy (Michaletz, Johnson, Mell, & Greene, 2013; Pounden, Greene, & Michaletz, 2014). Proximate causes of masting in white spruce are well known (Krebs, LaMontagne, Kenney, & Boutin, 2012; Roland, Schmidt, & Johnstone, 2014) and a relatively large amount of seed production data is available for this species since the second half of the 20th century across the North American boreal region (Pearse, LaMontagne, & Koenig, 2017).

Methods

2.1. The study case

White spruce is a masting species that naturally grows over large areas of boreal Canada and Alaska. The frequency of good cone crops is not stationary in time, varying from 2 to 12 years

depending on the time period considered and site characteristics (Juday et al., 2003; Lamontagne & Boutin, 2007; Roland et al., 2014). Interestingly, white spruce persists under a crown-fire regime (Michaletz et al., 2013; Pounden et al., 2014) despite lacking of fire-related adaptations such as sprouting, heat- or smoke-stimulated flowering or seed germination, or serotiny as it is the case for its associated trees such as the serotinous *Picea mariana* (Mill.) B.S.P. The apparent lack of fire-related adaptations in white spruce makes "its widespread distribution in fire-prone boreal forests perplexing" (Abrahamson, 2005). However, it is well documented that when white spruce masting follows a fire disturbance, the regeneration pulse is remarkable (Peters et al., 2005; Purdy et al., 2002). Through fire, the reduction of coarse or refractory organic material from the forest floor significantly improves white spruce seed germination, seedling growth and establishment (Greene et al., 2007; Zasada, Sharik, & Markku, 1992). Although white spruce may display a transient aerial seed bank in closed cones that protect seeds from heating during crown fire (Michaletz et al., 2013; Pounden et al., 2014) the regeneration success in burned zones highly depends on the quantity of seeds available in surviving seed trees, particularly in fire skips and surrounding unburned areas (Galipeau, Kneeshaw, & Bergeron, 1997; Greene et al., 1999; Pounden et al., 2014). Likewise, recruitment success decreases with increasing time since fire (Peters et al., 2005; Purdy et al., 2002), highlighting the importance of the timing of masting in relation to fire disturbance.

The proximate causes of masting in white spruce are well described (Juday, Barber, & Zasada, 2003; Krebs et al., 2012; Roland et al., 2014). Drought stress and warm temperature anomalies induce the differentiation of bud primordia into reproductive staminate and ovulate buds, and several studies found a positive relationship between warm-dry weather and seed crop the following year (Krebs et al., 2016; Roland et al., 2014; Zasada et al., 1992). Large-scale fire disturbances over North American boreal forests are also triggered by warm-dry weather (Kitzberger et al., 2007). Several studies found a significant negative correlation between the Palmer Drought Severity Index (hereafter Drought index) in summer and the annual burnt area (Shabbar, Skinner, & Flannigan, 2010; Xiao & Zhuang, 2007). Widespread drought over large portions of North American boreal forests are linked to climate modes of sea surface temperatures such as El Niño-Southern Oscillation (ENSO) and Atlantic Multidecadal Oscillation (AMO), with significant correlations at both inter-annual and decadal time scales (Shabbar &

Skinner, 2004). These teleconnections might synchronize fire disturbance in this region (Beverly, Flannigan, Stocks, & Bothwell, 2011; Hess et al., 2001; Shabbar et al., 2010). Indeed, when ENSO and AMO are both in a positive phase (Enfield, Mestas-nunez, & Trimble, 2001; Mo, Schemm, & Yoo, 2009), their coupled effect seems responsible for synchronous drought (Shabbar & Skinner, 2004) and fire activity over western North America (Kitzberger et al., 2007).

2.2. Workflow and hypotheses tested

We tested the hypothesis that the same climate drivers synchronize both masting and fire disturbance (hereafter the "synchronization hypothesis") in the North American boreal forest at both inter-annual and decadal time scales. At an inter-annual timescale, the synchronization hypothesis states that a mast year (T) has a high probability of occurrence after large fire disturbance in the year before (T-1). Particularly, we tested the following potential correlations (Figure 1): i) The Drought index at T-1 inversely correlates with burnt area in year T-1 and masting in year T; ii) masting at T correlates positively with area burnt the year before (T-1); iii) the coupling of positive phases of both ENSO and AMO (AMO+/ENSO+) positively correlates with the Drought index, burnt area at year T-1 and masting at T.

We additionally tested the consistency of the synchronization hypothesis on a decadal temporal scale verifying if long-term oscillations in AMO+/ENSO+ teleconnections are coherent to decadal variation in the Drought index, burnt area and masting.

2.3. Data collection

Time series of cone and seed data are available for white spruce for selected sites across the North American boreal region starting from the second half of the 20th century (Pearse et al., 2017). These data were supplemented by an additional exhaustive review of the scientific literature, and some unpublished records. In total the assembled database included 1062 yearly observations spanning four regions of North America (Alaska, USA; and Yukon, Alberta, and Quebec in Canada) (Figure 2) and the time period 1950 to 2017. Because several sources used the same raw data (Juday et al., 2003; Krebs et al., 2016; Lamontagne & Boutin, 2007; Roland et al., 2014), duplicated data were filtered out. Also, continuous seed production series shorter than eight consecutive years were excluded from further analysis, to avoid bias introduced by

short time series. We ended up with a total of 771 distinct yearly observations (data are available on FigShare, see the "Data availability" section).

Data of yearly burnt area for the Canadian part of the study region were retrieved from the Canadian National Fire Database (Canadian Forest Service, 2017). We used data spanning from 1950 to 2017 for Yukon and Alberta, and from 1973 to 2017 for Quebec. Yearly burnt area for Alaska was obtained from the Large Fire Database of the Alaska Fire Service, which dates back to 1950 (Kasischke & Turetsky, 2006).

Gridded values of monthly Palmer Drought Severity Index based on Penman-Monteith potential evapotranspiration with a spatial resolution of 2.5° for the period 1850-2014 were downloaded from public sources (Dai, 2011).

For the ENSO teleconnection we used the Oceanic Niño Index for the years 1950–2017 obtained by the Climate Prediction Centre of the National Oceanic and Atmospheric Administration (NOAA) of USA. This index corresponds to 3 month running mean of sea surface temperature anomalies in the Niño 3.4 region (5°N-5°S, 120°-170°W) based on centered 30-year base periods updated every 5 years using the Extended Reconstructed Sea Surface Temperature, version 5 (ERSST.v5). The unsmoothed monthly AMO index (Enfield et al., 2001) for the years 1950–2017 was obtained by the Earth System Research Laboratory of NOAA.

The white spruce distribution range within the study area was retrieved in a digital format from the US tree Atlas (Little, 1971).

2.4. Data processing

The masting database for white spruce included both ordinal and continuous seed series in different classes and units, respectively. Consequently, we harmonized all series to maximize the amount of data available for analyses. Raw ordinal data were harmonized using a five class system (1: no masting; 5: mast year) as in Ascoli, Maringer et al. (2017); raw continuous series were square-root transformed and re-classified to the 5 class ordinal scale by dividing the data range into 5 equal intervals. Drought index and fire data did not require harmonization. To carry out the analyses presented in section 2.5., harmonized masting series (ORDmast column in the database available on FigShare), Drought index and fire data were aggregated at different spatial scales (regional and sub-continental) as defined below.

2.4.1. *Data aggregation at regional scale*

To analyze data series (fire, drought, masting) at the same spatial unit we aggregated data at the regional scale (i.e., the province/state level: Alaska, Yukon, Alberta and Quebec), since fire data were provided at this scale. In addition, this data aggregation allowed us to obtain long masting chronologies and minimize gaps in our regional time-series (Vacchiano et al., 2017).

Regional Drought index series for each region were computed by averaging values for July (i.e., month of bud differentiation) over the white spruce distribution range within Alaska, Yukon, Alberta, and Quebec.

We ran a Mantel test to determine the appropriate spatial scale for aggregation of cone production data. We calculated ranked (Spearman) correlations between dissimilarities of masting time series and geographic distance between sites. The existence of spatial aggregation in white spruce masting was confirmed by significantly positive ($P < 0.01$) Mantel correlation coefficients ($M= 0.73$) and decreasing similarity between cone production time series with increasing distance between them (Supplementary Figure S1). Some sites were represented by multiple series (e.g., different survey plots at the Bonanza Creek site). As a marked correlation was observed at a fine scale (i.e. similarity > 0.6 at 10-20 km distance), we first aggregated such series into site chronologies (SCs) by using the most frequently observed masting class for each year at a given site (e.g., Bonanza Creek). This was necessary to avoid assigning a higher weight to sites with many series (e.g., different stands surveyed at the Bonanza Creek site) relative to less intensively sampled sites. SCs were then aggregated into regional chronologies (RCs) by using the most frequently observed masting class for each year in a region (i.e., Alaska, Yukon, Alberta, Quebec). In the case of two or more masting classes displaying the same frequency in a given year, we selected the highest masting class or the intermediate, respectively. The final ordinal RCs were 49 years for Alaska (1957 to 2016), 28 years for Yukon (1987 to 2016), 61 years for Alberta (1951 to 2016) and 23 years for Quebec (1989 to 2014) (Table S1).

2.4.2. *Data aggregation at sub-continental scale*

To test for correlations with AMO and ENSO, we computed the Drought index, fire and masting indices at a sub-continental scale which is the adequate spatial approach to analyze how

teleconnections influence both geophysical and ecological phenomena (Beverly et al., 2011; Forchhammer & Post, 2004; Mysterud et al., 2003). However, since the influence of AMO and ENSO is primarily exerted on western North America (Supplementary Figure S2) with minor influence on eastern regions (Shabbar & Skinner, 2004), and we observed no positive correlations between cone production in eastern and western Canada (Supplementary Figure S1), the province of Quebec was excluded from the sub-continental scale that finally included the western regions Alaska, Yukon, and Alberta only. The sub-continental fire index was computed by averaging standardized yearly regional series of burnt area and the sub-continental Drought index was computed by averaging values of the Drought index for July over the white spruce distribution range within the western regions considered.

A continuous masting index at the sub-continental scale, as required for statistical analyses at this scale (see section 2.5), was computed as follows: we computed for each year the difference between the proportions of ordinal site chronologies (SCs) displaying a full mast (class 5, SC-5) and a poor masting (classes 1 and 2, SC-12) after Ascoli, Vacchiano, et al., (2017). This difference generates a continuous index that varies from −1, when all SCs are in class 1 and 2 (broad masting failure), to +1 when all SCs are in the masting class 5 synchronously throughout Alaska, Yukon and Alberta. Intermediate (zero) values indicate a prevalence of classes 3 and 4, or a balanced distribution of SC-5 and SC-12 (Table S1). The resulting continuous masting index at the sub-continental scale (M_index) covered 59 years from 1957 to 2016 (Table S1).

Since ENSO warm phases (El Niño phase) from winter to summer strongly influence sea surface temperature and air pressure, temperature and moisture in the western North America, particularly during positive phases of AMO (Supplementary Figure S2), we used the December to August values of both the Oceanic Niño Index and AMO indices. A coupled AMO+/ENSO+ index was computed by running a Principal Component Analysis of the two indices. The yearly scores of the component correlated positively to both ENSO and AMO were used as AMO+/ENSO+ index.

2.5. Statistical analyses

To examine the temporal association between masting, fire, and drought at the inter-annual temporal scale we used Superposed Epoch Analysis (Baisan & Swetnam, 1990). This test compares the mean values of given environmental variables before, during or after an event with

the mean of the same variables across non-event years. The comparison is based on Monte Carlo simulations that randomly pick years, calculate expected means, and provide 95% bootstrap confidence intervals. The technique has often been applied to analyze relationships between climate and ecosystem response, e.g. climate and fire events (Grissino-Meyer et al., 2004), or drought and tree mortality (Gea-Izquierdo et al., 2014). Here, we used Superposed Epoch Analysis for each region separately to assess if the burned area and the Drought index in years before a masting event were significantly different from those recorded in other years. Burned area and Drought index were calculated for a 7-year window centered on the mast year. The number of randomly selected non-masting years used in the comparison was equal to the number of actual masting years. We identified mast events by selecting years displaying a masting class 5 (Table S1). To test for the relationship between fire disturbance and drought we also ran separate superposed epoch analyses for each region, using burnt area as the dependent variable and years in which the Drought index was < its 20th percentile as drought events.

To investigate the coupled effect of AMO and ENSO at the sub-continental scale, we defined AMO+/ENSO+ events, i.e., when El Niño years (warm phase of ENSO) coincided with a positive phase of AMO according to the classification provided in Table 1. Then, we ran separate superposed epoch analyses to assess if M_index, the Drought index and fire indices at the sub-continental scale were significantly different than those one to three years before and after an AMO+/ENSO+ event (3-yr lag). All superposed epoch analyses were performed using the package "dplr" (Bunn 2008) within the R statistical framework (R Core Team, 2019). Bootstrap resampling was used to randomly select sets of lag+1 years from the data set and to estimate significances for the departures from the mean.

Table 1 - Years identified as Cool and Warm episodes for Atlantic Multidecadal Oscillation (AMO) and El Niño Southern Oscillation (ENSO) (1950–2016). El Niño events (i.e. positive phase of ENSO) are defined as 5 consecutive overlapping 3-month periods at or above the +0.3° anomaly of the Oceanic Niño Index along the winter to summer seasons. AMO+ years corresponds to positive values of the AMO index. Numbers in bold corresponds to AMO+/ENSO+ event years used for superposed epoch analyses in Figure 4.

	AMO	ENSO	AMO+/ENSO+ events
Cool episodes Negative phase (AMO-; La Niña)	1964-1968, 1970-1986, 1989-1994	1950, 1954, 1955, 1964, 1967, 1970, 1971, 1973, 1974, 1975, 1984, 1988, 1995, 1999, 2000, 2005, 2007, 2008, 2010, 2011	
Warm episodes Positive phase (AMO+; El Niño)	1950-1963, 1969, 1987-1988, 1995-2016	1953, 1957, 1958, 1966, 1969, 1982, 1983, 1987, 1991, 1992, 1997, 1998, 2002, 2004, 2015, 2016	1951, 1953, **1957, 1958, 1969, 1987, 1997,1998, 2002, 2004, 2015, 2016**
Neutral phase		1951, 1952, 1956, 1959, 1960, 1961, 1962, 1963, 1965, 1968, 1972, 1976, 1977, 1978, 1979, 1980, 1981, 1985, 1986, 1989, 1990, 1993, 1994, 1996,	

To test whether decadal oscillations in teleconnections are correlated to long-term trends in masting patterns, drought and fire disturbance at the sub-continental scale we carried out wavelet coherence analysis (Cazelles et al., 2008). Coherence is a measure of the intensity of the covariance of two series in the time-frequency space. The test measures the cross-correlation between two series as a function of time and frequency, allowing the identification of time-localized common oscillatory behavior. Wavelet coherence is well suited to detect localized correlations of non-stationary signals (Grinsted, Moore, & Jevrejeva, 2004) such as teleconnection indices, drought, fire or masting, i.e. series that display a variable frequency through time (Ascoli, Vacchiano, et al., 2017). For these reasons, wavelet coherence has often been used to test for relationships between climatic teleconnections and geophysical and ecological processes (Grinsted, Moore, & Jevrejeva, 2004).

The use of wavelet coherence required computation of the continuous M_index at the sub-continental scale (see section 2.4.1.). To avoid bias due to non-normality, burnt area and M_index were arcsine-transformed before the wavelet analysis. The analysis was limited to the period 1957-2016 (i.e., the temporal domain of the M_index). Each wavelet coherence analysis was computed with the *wtc* function in the R package "biwavelet" (Gouhier, Grinstead, & Simko, 2016) using a Morlet continuous wavelet transform and considering the lag−1 autocorrelation of each series. The data were padded with zeros at each end to reduce wraparound effects

(Grinsted, Moore, & Jevrejeva, 2004). Significance of coherence at all frequencies lower than three years was tested using a time-average test with 2000 Monte Carlo randomizations.

Results

Superposed Epoch Analyses showed that in each region (Alaska, Yukon, Alberta, Quebec) burnt area was significantly higher during drought events (i.e., July-Drought index < 20th percentile) in all regions (Figure 3, first row), and was on average 322% higher than in non-drought years. Consistent with our hypotheses, the July-Drought index was significantly lower than average for the year T-1, i.e. the year before a mast event (Figure 3, second row). Consistent with these results, in each considered region (Alaska, Yukon, Alberta, Quebec) the year before a mast event (T-1) showed a significant positive departure from mean burnt area (Figure 3, third row).

During AMO+/ENSO+ events (see Table 1, years indicated in bold) both sub-continental indices of Drought index and burnt area across boreal regions of western North America experienced significant departures from mean values (Figure 4). The same was observed for the M_index in the subsequent year.

Wavelet coherence between teleconnections indexes (both ENSO and AMO+/ENSO+) and M_index, burnt area and the Drought index at the sub-continental scale from 1957 to 2016 showed a significant coherence (Figure 5), which shifted from a frequency domain of 8 - 11 before 1990 to a frequency of 3 - 6 years in more recent decades (red regions with black contours in the graph). In most periods, wavelet coherence showed an in-phase fluctuation between teleconnections and sub-continental indices led by ENSO or AMO+/ENSO+ (arrows pointing up and right). In comparison to ENSO, the AMO+/ENSO+ index had a stronger coherence with M_index and burnt area, but a weaker relationship with the Drought index. Notably, a wavelet coherence analysis between the Drought index and burnt area (Figure S3A), and between burnt area and M_index (Figure S3B), displayed a similar non-stationary pattern, with lower frequencies before 1990 (around 11 years) and higher frequencies from 1990 to 2000.

Discussion

Inter-annual time scale at regional level

Masting events in white spruce tended to occur in the year after summer drought in the studied regions across North America. This is consistent with previous observations of the temperature and precipitation regulation of reproduction in the genus *Picea* (Ascoli et al., 2017; Juday et al., 2003; Krebs et al., 2016; Roland et al., 2014; Selås, Piovesan, Adams, & Bernabei, 2002), confirming that high summer temperatures and aridity at year T-1 (i.e., low values of the Palmer Drought Severity Index) act as climatic cues of reproductive bud initiation, which results in mast seeding in year T.

In accordance with previous studies (Shabbar et al., 2010; Xiao & Zhuang, 2007) we also report a strong association between warm-dry conditions in summer (low values of the Palmer Drought Severity Index) and regional burnt area in all studied North American boreal regions. Interestingly, drought intensity triggering both masting and fire was comparable: the Superposed Epoch Analysis showed that drought intensity in years preceding masting events (mean July-Drought index = -1.43) is similar to the intensity in years with a significantly higher burnt area (mean July-Drought index = -1.48).

Notably, the initial hypothesis of a positive correlation between regional masting at year T and regional burnt area the year before at T-1 (Figure 1) was confirmed. Previous studies investigating the persistence of white spruce in boreal crown-fire regimes stressed the importance of a coincidence between fire and cone production in the same year (Michaletz et al., 2013; Pounden et al., 2014), rather than the year before (T-1) as found in the current study. Under the hypothesis that closed cones protect the transient aerial seed bank during a crown-fire, the authors calculated that the probability for white spruce to bear closed cones during a mast event in coincidence with crown-fire disturbance ranged from 5% (Michaletz et al., 2013) to 10% (Pounden et al., 2014). The capacity of white spruce to occasionally behave as an aerial seed bank species is complementary to our hypothesis, but our results show that fire precedes masting more frequently than when they occur in the same year (Figure 3). Indeed, as a consequence of the same drought trigger, the year before a mast event was more likely to experience a significantly positive departure from mean burnt area in all studied regions.

To our knowledge, no prior study has shown a correlation between reproduction in a masting tree species and previous year fire extent. A few studies in fire-prone regions of Australia found that seed production in grass and shrub species displaying heat stimulated seed

germination (*Triodia spp.* and *Acacia aptaneura*, respectively) was strongly related to increased fire likelihood in the 24 months after the reproduction event (Wright & Fensham, 2017; Wright et al., 2014). Similarly to our results for white spruce, in these studies the same climate cue (precipitation in previous months) was responsible for both the induction of flowering and the increase of burnt area, due to fuel build-up and improved fuel connectivity after moist years. A significant increase in burnt area has also been observed after widespread reproduction of bamboo in South-East Asia (Fava & Colombo, 2017), although in this case fire is not driven by weather, but rather by the increase in fuel that followed post-reproduction mortality of bamboo over large areas.

Sub-continental scale

AMO is the dominant mode of long-term sea surface temperature variability in the Atlantic Ocean that strongly influences Walker circulation in the tropical Pacific Ocean and modifies ENSO stability over both annual and decadal time spans (Levine, McPhaden, & Frierson, 2017; Enfield, Mestas-nunez, & Trimble, 2001). Our results suggest that synchronous drought and fire activity across the studied regions occur when warm phases of AMO and ENSO coincide. This is consistent with previous studies on the coupled effect of warm phases of these two teleconnections (AMO+/ENSO+) on soil moisture content (Shabbar & Skinner, 2004) and synchronous wildfire activity (Kitzberger et al., 2007) across boreal regions of western North America.

Consistent with our initial hypotheses (Figure 1), the sub-continental scale masting index is significantly higher one year after AMO+/ENSO+ events, i.e., one year after synchronous drought and fire activity. Several teleconnection indices were found to correlate with masting and its proximate causes in many tree species and geographical regions, such as the North Atlantic Oscillation for beech (*Fagus sylvatica* L.) and spruce (*Picea abies* (L.) H.Karst.) in Europe (Ascoli et al., 2017) or ENSO for Dipterocarpaceae in East Asia and Oceania (Chechina & Hamann, 2019). However, due to the limited availability of seed production data, the effect of the low-frequency component of such teleconnections has been rarely tested.

Additionally, we showed that decadal changes in AMO+/ENSO+ displayed common oscillatory trends with fire and white spruce masting series in the last 60 years. The frequency with which

these processes co-varied was not periodic but displayed a non-stationary signal with frequencies shifting from 8-11 years towards shorter periods near the mid 1990s. This result highlights the potential role of AMO and ENSO coupling in modulating common shifts in the frequency of both fire disturbance and *Picea glauca* reproduction, not only at inter-annual intervals but also at a decadal time scale. The synchronization between periods of increased fire activity and periods of more frequent large-scale masting would provide white spruce with a strong competitive advantage for its reproduction and long-term persistence in a crown-fire prone environment and a higher adaptability to changes in fire regimes driven by climate changes.

Ecological and evolutionary implications

Juday et al. (2003) speculated that white spruce maximizes the odds that seeds will be released into a recently burnt landscape based on the existence of a common trigger for floral induction and fire disturbance (i.e. summer drought). Indeed, a positive interaction exists between the timing of masting in white spruce and short-term crown-fire effects (Greene et al., 2007; Peters et al., 2005; Purdy et al., 2002). Trees along fire edges or in fire skips, as well as few large surviving individuals in burnt areas, function as seed trees in a post-fire environment (Pounden et al., 2014) and may behave as super-producers accounting for a large portion of overall seed production (Hacket-Pain et al., 2019; Minor & Kobe, 2017). Seeds dispersed shortly after fire germinate more easily due to partial litter consumption, and seedlings can establish more successfully due to canopy openings and lower competition relative to unburnt stands (Peters et al., 2005; Purdy et al., 2002). Such positive feedback has been observed in many other masting tree species whose reproduction is facilitated by forest canopy gaps and soil disturbance (Maringer et al., 2020; O'Dowd & Gill, 1984; van Mantgem et al., 2006). It has also been noted that for some species the proximate causes triggering masting are also associated with an increased probability of natural fire disturbance, e.g., stand aging and dead fuel accumulation in bamboo (Keeley & Bond, 1999), dry and hot spells in Norway spruce (Selås et al., 2002), European beech (Ascoli et al., 2015) and Dipterocarpaceae (Williamson & Ickes, 2002), or heavy rains followed by warm periods in *Triodia* spp. (Wright et al., 2014) and *Acacia aptaneura* (Wright & Fensham, 2017). Most of these authors have suggested that this positive feedback supports

the “Environmental prediction hypothesis” for mast seeding (Piovesan & Adams, 2005), which postulates the existence of traits that benefit plants in timing their seed crops by using environmental cues to ‘predict’ which years will be favorable for seedling establishment. As a consequence, these traits may represent the result of a positive selection during evolution. Our findings that seed production follows fire-prone years in *Picea glauca* suggest the possibility that a fire-related form of environmental prediction hypothesis exists in this tree species. However, for such a masting phenology to have evolved, drought and fire must have been correlated with each other in boreal forests for an evolutionarily significant time. This seems highly likely, as increased flammability following drought is an intrinsic feature of circumboreal forest ecosystems (Aakala et al., 2018; Eichler et al., 2011; Kitzberger et al., 2007) that may have existed ever since boreal conditions emerged during the Cretaceous period, following the breakup of Pangaea starting 200 million years ago (Mauseth, 2014). The origin of *Picea* in North America dates back to the early Tertiary or late Cretaceous (100.5-66 million years before present) (Ran, Wei, & Wang, 2006), a period of marked global fire activity, including boreal regions (Bond & Scott, 2010). *Picea* persisted in these regions during the last glacial maximum (Zazula, Telka, Harington, Schweger, & Mathewes, 2006) and sedimentological records indicate that in the Lateglacial the appearance of *P. glauca* coincided with increased charcoal indicators of fire (Anderson et al., 2006) with decreased fire return intervals ranging from 200 to 380 years (Tinner et al., 2006). It is likely that white spruce faced recurrent drought-driven fires throughout its evolutionary history. On top of the drought and fire correlation, trees that produced large seed crops in coincidence with suitable post-fire conditions for an increased seed viability, germination, and establishment would be favored evolutionarily. Indeed, when the drought cue synchronizes mast crops soon after large fire years it creates an economy of scale (Koenig & Knops, 1998), i.e., successful offspring, that might reinforce the feedback loop between the climate pattern and masting (Brunner, Deere, Egas, Eizaguirre, & Raeymaekers, 2019; Moreira, Abdala-Roberts, Linhart, & Mooney, 2015) through directional selection on masting traits in white spruce.

Conclusions

In this study we used long-term data of white spruce masting, drought and burnt area in the North-American boreal forests to test the extent to which these processes are synchronized by common large-scale climate patterns (i.e. teleconnections) at both inter-annual and decadal time scales. We report the existence of a common driver (i.e. summer drought) shared by fire and masting. We furthermore showed significant correlations between the coupled effect of positive phases of the Atlantic Multidecadal Oscillation and of the El-Niño Southern Oscillation drought and fire disturbance on one side, and between white spruce masting and previous-year burnt area on the other.

Climate changes will modify large scale climate patterns such as the Atlantic Multidecadal Oscillation and the El-Niño Southern Oscillation, and related biophysical processes such as fire disturbance (Mariani et al., 2018; Seidl et al., 2017) and plant reproduction (Ascoli et al., 2017; Koenig & Knops, 1998). Future changes in fire regimes might be an important driver of boreal ecosystems processes (Kasischke & Turetsky, 2006) affecting species that lack fire adaptive traits such as *Picea glauca*. However, white spruce might show some adaptability to changes in climate teleconnections via the synchronization of its seed crops with changes in disturbance regimes, which provide this fire-sensitive species with higher than expected plasticity and climate adaptation capacity.

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Figure legend section

Figure 1 – Scheme of inter-annual (A) and decadal (B) correlations tested in the present study. A) The rectangle represents the inter-annual synchronization among climate teleconnections, drought, fire, and masting. B) The blue line represents decadal variation in climate oscillations and white rectangles the occurrence of an inter-annual synchronization between fire and masting (scheme A). Solid arrows in the rectangle indicate correlations tested at regional level whereas dashed arrows refer to correlations tested at sub-continental level. Relationships indicated in red are not tested in the present study but have been demonstrated in previous studies (Peters et al., 2005; Purdy et al., 2002).

Figure 2 – Map showing the study area. Acronyms indicate the investigated provinces and states: Alaska (AK), Yukon Territory (YT), Alberta (AB) and Quebec (QC). The green area represents the white spruce distribution across western North America gathered from the US tree Atlas (Little, 1971). Red polygons show synchronous wildfires across western North America in year 2004 in coincidence of a positive phase of both El Niño Southern Oscillation and the Atlantic Multidecadal Oscillation teleconnections (see Table 1). Yellow dots indicate the location of masting site chronologies used in the study (see Table S1). Fire perimeters were provided by the Canadian National Fire Database (Canadian Forest Service, 2017). The white spruce distribution range within the study area was retrieved in a digital format from the US tree Atlas (Little, 1971).

Figure 3 – Results of the Superposed Epoch Analyses at regional scale. First column: Alaska (period 1955-2014); second column: Yukon (period 1984-2014); third column: Alberta (period 1948-2014); forth column: Quebec (period: 1987-2014). First row: burnt area vs. July-Drought index events (<20th percentile of regional series). Second row: July-Drought index vs. mast events (class 5). Third row: burnt area vs. mast events (class 5). The number of events is reported on each bar graph (n=). Black bars indicate significant departure from the mean. Significance levels are: *** p<0.001; **p<0.01; *p<0.05.

Figure 4 – Results of the Superposed Epoch Analyses at sub-continental scale using the coupled El Niño Southern Oscillation and Atlantic Multidecadal Oscillation index (AMO+/ENSO+). Left: July-Drought index vs. AMO+/ENSO+ events (warm AMO coupling with warm ENSO, 1957-2016). Centre: burnt area vs. AMO+/ENSO+ events. Right: M_index vs. AMO+/ENSO+ events. The number of AMO+/ENSO+ events used was 10 (see Table 1, years indicated in bold). Black bars indicate significant departure from the mean. Significance levels are: *** $p<0.001$; **$p<0.01$; *$p<0.05$.

Figure 5 - Wavelet coherence between the masting index (M_index), Burnt area and Drought indices at the sub-continental scale with the winter El Niño Southern Oscillation index (ENSO) and with the coupled El Niño and Atlantic Multidecadal Oscillation index in the positive phase (AMO+/ENSO+): A) ENSO vs. M_index. B) AMO+/ENSO+ vs. M_index. C) ENSO vs. Burnt Area. D) AMO+/ENSO+ vs. Burnt Area. E) ENSO vs. Drought index. F) AMO+/ENSO+ vs. Drought index. Areas of strong coherence in time and frequency scales between series are shown in red. Black contours designate frequencies of significant coherence ($p < 0.1$, two-sided test) against red noise. Lighter shading shows the cone of influence where edge effects are important. Arrows pointing up and right show in-phase behavior and teleconnections leading masting, burnt area and the Drought index (please note that the Palmer Drought Severity Index has been changed in sign to aid interpretation).

Data availability

Data are published on FigShare with the following DOI: 10.6084/m9.figshare.8870288

and can be accessed at:

https://figshare.com/articles/Picea_glauca_masting_data_across_North_America/8870288

Data sources

The Oceanic Niño Index for the years 1950–2016 obtained by the Climate Prediction Centre of the National Oceanic and Atmospheric Administration (NOAA) of USA. URL:

https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php (last access: 03/08/2019). The unsmoothed monthly AMO index (Enfield et al., 2001) for the years 1950–2016 was obtained by the Earth System Research Laboratory of NOAA. URL: https://www.esrl.noaa.gov/psd/data/correlation/amon.us.data (last access: 03/08/2019).

Author contribution

A.D., A.H.P., J.L.M., G.V. and M.C. conceived the ideas and designed methodology; J.L.M., P.I.S., A.H.P. and A.D. collected the data; A.D. and G.V. analyzed the data; A.D. led the writing of the manuscript with contribution from all co-authors. All authors contributed critically to the drafts and gave final approval for publication.

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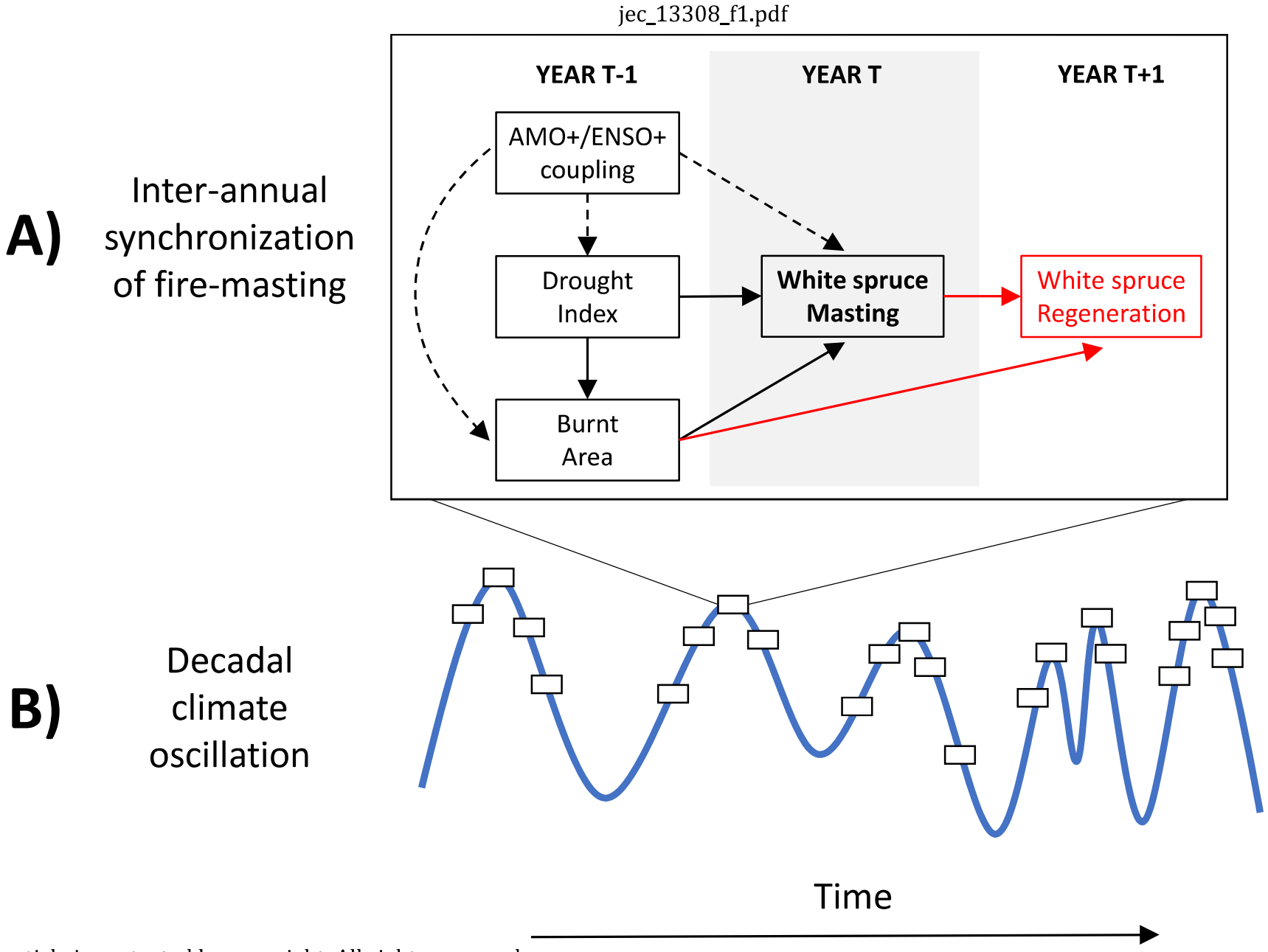

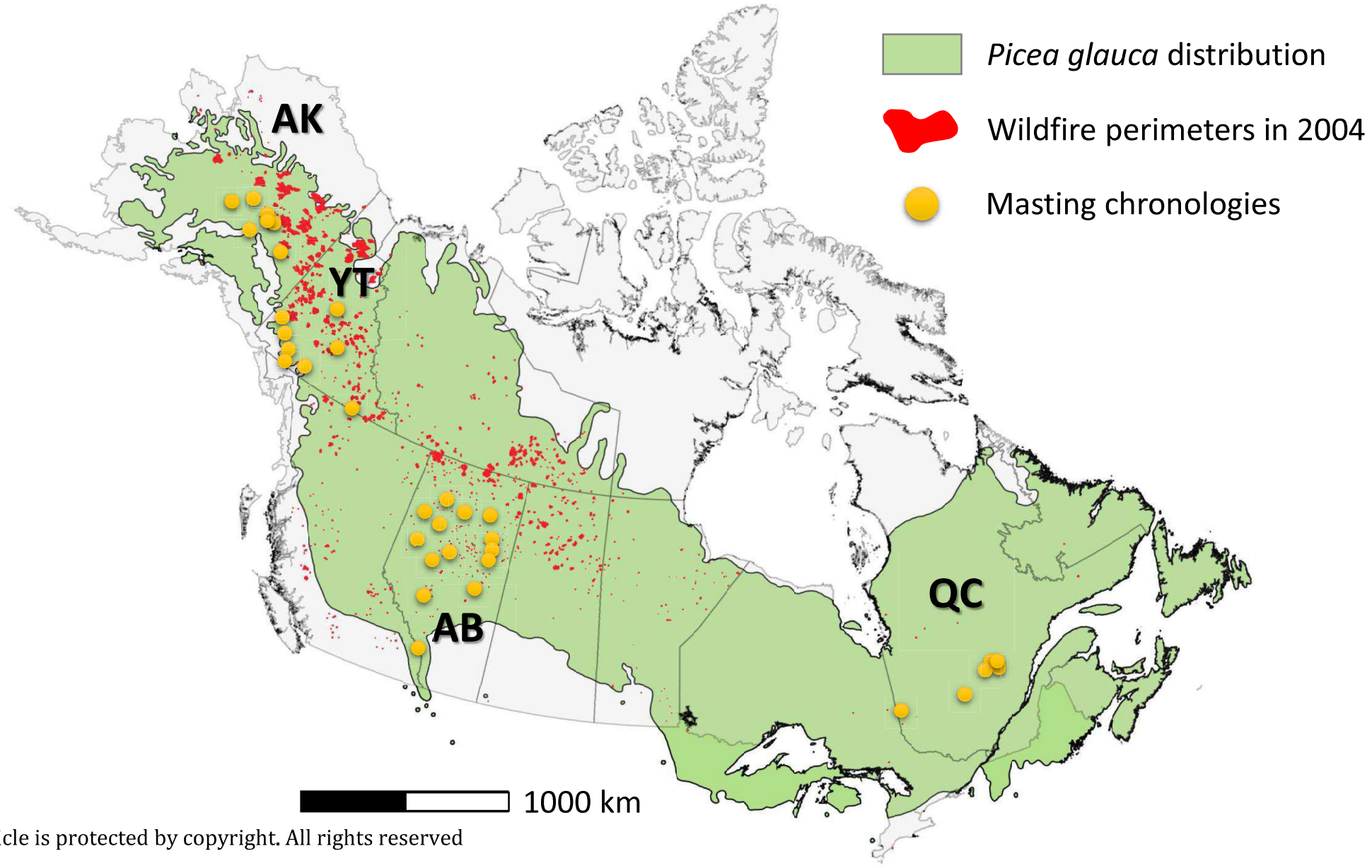

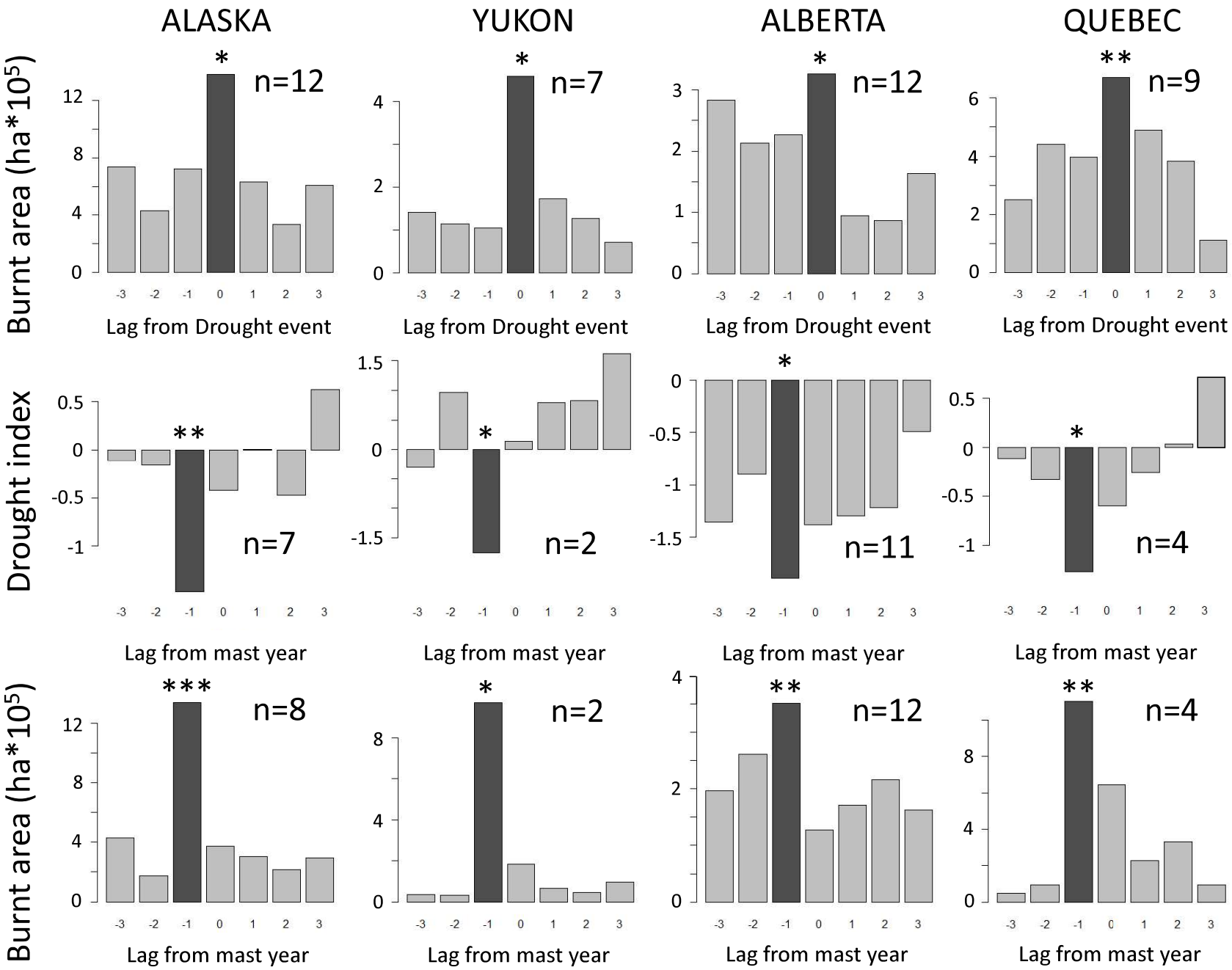
ALASKA
YUKON
ALBERTA
QUEBEC
Burnt area (ha*10^5)
Drought index
Burnt area (ha*10^5)
n=12
n=7
n=12
n=9
n=7
n=2
n=11
n=4
n=8
n=2
n=12
n=4
*
**
***
Lag from Drought event
Lag from mast year